CHARACTERIZING THE TAPHONOMICALLY ACTIVE ZONE IN SUBTROPICAL PEAT FROM BARNES SOUND IN KEY LARGO, FLORIDA

A Thesis

by

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ABSTRACT

Surficial mangrove peat from Barnes Sound in Key Largo, Florida preserves very thick leaf mats (19-37 stacked leaves). The incoherent leaf mat occurred below the coherent leaf mat to a depth of approximately 5 cm, and consisted of degraded and fragmented leaves intruded by living horizontal and vertical rootlets. Short cores (13 cm deep) indicated that the peat below the coherent and incoherent leaf mat consists primarily of living and dead roots and rootlets, large pieces of wood, and fecal pellets.

Taphonomic analysis of 100 leaves from the coherent leaf mat at Barnes Sound indicated that fallen leaves record canopy herbivory and parasitism, as well as the decomposition pathways occurring on the mire surface: microbial decomposition and detritivory by snails. Canopy herbivory and parasitism by micro-arthropods, insects and the mangrove crab was most prominent. Abundant fecal pellets (106 μm – 2 mm), edge feeding, and skeletonization in the coherent and incoherent leaf mats indicated the importance micro-detritivores. Shells belonging to the detritivorous neogastropod *Melampus coffeus* occurred in the core, but leaf deterioration by *M. coffeus* was hard to distinguish. Leaves showing attack patterns characteristic of detritivorous mangrove crabs appeared in the coherent leaf mat, but no crab burrows appeared on the mire surface.

Macro-detritivores (specifically crabs) play an important role in the decomposition pathways in many modern mangrove mires. Mangrove peat at Barnes Sound preserved an exceptionally thick leaf mat, possibly due to the scarcity of

detritivorous mangrove crabs at this locality. If crabs are reduced or absent, thick leaf mats can accumulate in saltwater mires. Our results indicate that in the absence of these and similar macro-detritivores, thick leaf mats could have accumulated in ancient saltwater mires. Low shoot-to-root ratios and the presence of thick leaf mats cannot confidently be used as taphonomic indicators of freshwater peat.

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1. INTRODUCTION

Pennsylvanian permineralized peats preserve very thick accumulations of aerial debris. Thick leaf mats have been suggested as indictors of mire habitat (freshwater or marine), water depth, and decomposition rate (Raymond et al., 1987; Covington and Raymond, 1989; Gastaldo and Staub, 1999; Raymond et al., 2001). The preservation of delicate plant parts has often caused controversy concerning the depositional environment of Pennsylvanian mires, specifically whether these were freshwater or saltwater. Comparing terrestrial plant ecosystems from Pennsylvanian mires to modern mires is useful in understanding how interactions in mire ecosystem have changed through time as well as learning about the habitat of Pennsylvanian mires (Dimichele et al., 1996). The ecology of terrestrial decomposition in peat-accumulating environments has changed since the Late Paleozoic. One of the possible reasons for the change is the evolution of modern soil arthopods (beetles, flies, modern roaches, termites: Raymond et al., 2001). Terrestrial detritivores, including oribatid mites, millipedes, collembola and primitive insects were present during the Pennsylvanian, but the detritivore community was likely less efficient than the modern community (Grimaldi and Engel, 2005). Large woody roots are found in Pennsylvanian surficial peat, implying that leaf mats persisted long enough for woody roots to grow. Today, woody roots seldom occur in surficial peat (within the leaf mat) of either freshwater or saltwater mires.

This study focuses on mangrove peat-accumulating environments, specifically a modern subtropical mangrove mire located southeast of Barnes Sound in Key Largo,

Florida. Surficial peat (the taphonomically active zone of the peat) was investigated to understand how decomposition pathways and herbivory affect the composition of the peat. Within the surficial peat, the abundance and taphonomy of the aerial debris, specifically the leaf mat and its aerial contents was analyzed. Leaf mat condition (relative thickness, leaf taphonomy), presence and location of vertical and horizontal roots, and the presence and distribution of fecal pellets are characterized. Leaf mats rarely occur in mangrove swamps and few taphonomic studies have focused on mangrove leaf mats. Barnes Sound on Key Largo, Florida belongs to a growing number of Florida mangrove mires studied with thick leaf mat (S. Davis, 2014, pers. comm., 19 December). Because they are rare, few studies have addressed leaf mats in mangrove settings. The taphonomy of wood and bark is not the focus of this study; Feller (1995) discusses the detritivores that most likely decompose wood.

In Indo-Pacific (Old World) tropical mangrove mires, grapsid and ocypodid crabs consume large amounts of dead leaves. They are one of the major factors controlling the amount of aerial debris left on the forest floor (Roberson and Daniel, 1989; Osborne and Smith, 1990; Smith et al., 1991; Skov and Hartnoll, 2002; Alongi, 2009). In the New World, ocypodid crabs, terrestrial neogastropods, and amphipods consume dead leaves (Beever et al, 1979; Twilley et al., 1997; Proffit and Devlin, 2005; Nagelkerken et al., 2007; Nordhaus and Wolff, 2007, Middleton and McKee, 2001). New World grapsids are not as abundant, but they can often be found as herbivores in mangrove canopies (Erickson et al, 2003; Nordhaus, 2004; Nordhaus and Wolff, 2007;Cannicci et al., 2008; Erickson et al., 2008; Alongi, 2009).

Decapods such as ocypodid, sesaramid, and grapsid crabs live in intertidal locations and have a poor fossil record (Feldmann and Schweitzer, 2006). However, the earliest undisputed crabs appeared in the early to mid-Jurassic (Schweitzer and Feldmann, 2010). The earliest ocypodid and grapsid crabs, which include the sesarmids, date to the late Eocene-Oligocene (ocypodids, Barnes, 1968; grapsids, Glaessner, 1969). Thus, the evolution of modern decapods (Jurassic) as well as neogastropods (Cretaceous) may have had a profound impact on peat accumulation and the burial of organic debris in mangrove mires, and as such constitutes a potential taphonomic change in marine mires and siliciclastic swamps. The evolution of these macro-invertebrates much later than the Paleozoic mires may skew modern to ancient mire comparisons. Just as the evolution of modern soil arthropods (beetles, flies, modern roaches, termites) may have changed decomposition pathways in freshwater mires, modern crabs and neogastropods may have changed decomposition pathways in marine mires and siliciclastic swamps. Their importance in modern mangrove mires suggests that decomposition pathways in saltwater mires has changed significantly since the Paleozoic.

2. LITERATURE REVIEW

2.1 The Taphonomic Active Zone of Peat

Surficial peat is the taphonomically active zone (TAZ) of peat-accumulating environments, analogous to the taphonomically active zone in marine shore environments (Aller, 1982; Powell et al., 1986; Davies et al. 1989). The length of time spent on the surface and in the TAZ determines if it is part of the preserved fossil assemblage (Aller, 1982). In order to become peat, organic matter must travel through the TAZ/taphonomically active zone (Fig. 1). A leaf mat is an accumulation of aerial debris from the canopy and underlying plants, primarily leaves, that builds up on the surface of the peat (i.e. in the TAZ). Leaf mats preserve ecological interactions in the TAZ of peat such as the taphonomic attributes that occur within the TAZ such as leaf damage types and decomposition pathways. In freshwater wetlands, leaf-mat thickness reflects the balance between community productivity and decomposition rates; in saltwater wetlands, relative leaf mat thickness reflects the balance among community productivity, decomposition rates and tidal export (Cohen and Spackman, 1977; Alongi, 2009).

Carboniferous permineralized peats (sometimes referred as coal balls) are deposits from coal seams that preserve significantly more aerial debris than modern peat deposits sampled (Cohen and Spackman, 1977; Raymond et al., 2001). Coal balls probably formed in the TAZ of Carboniferous and Early Permian peats, resulting in the

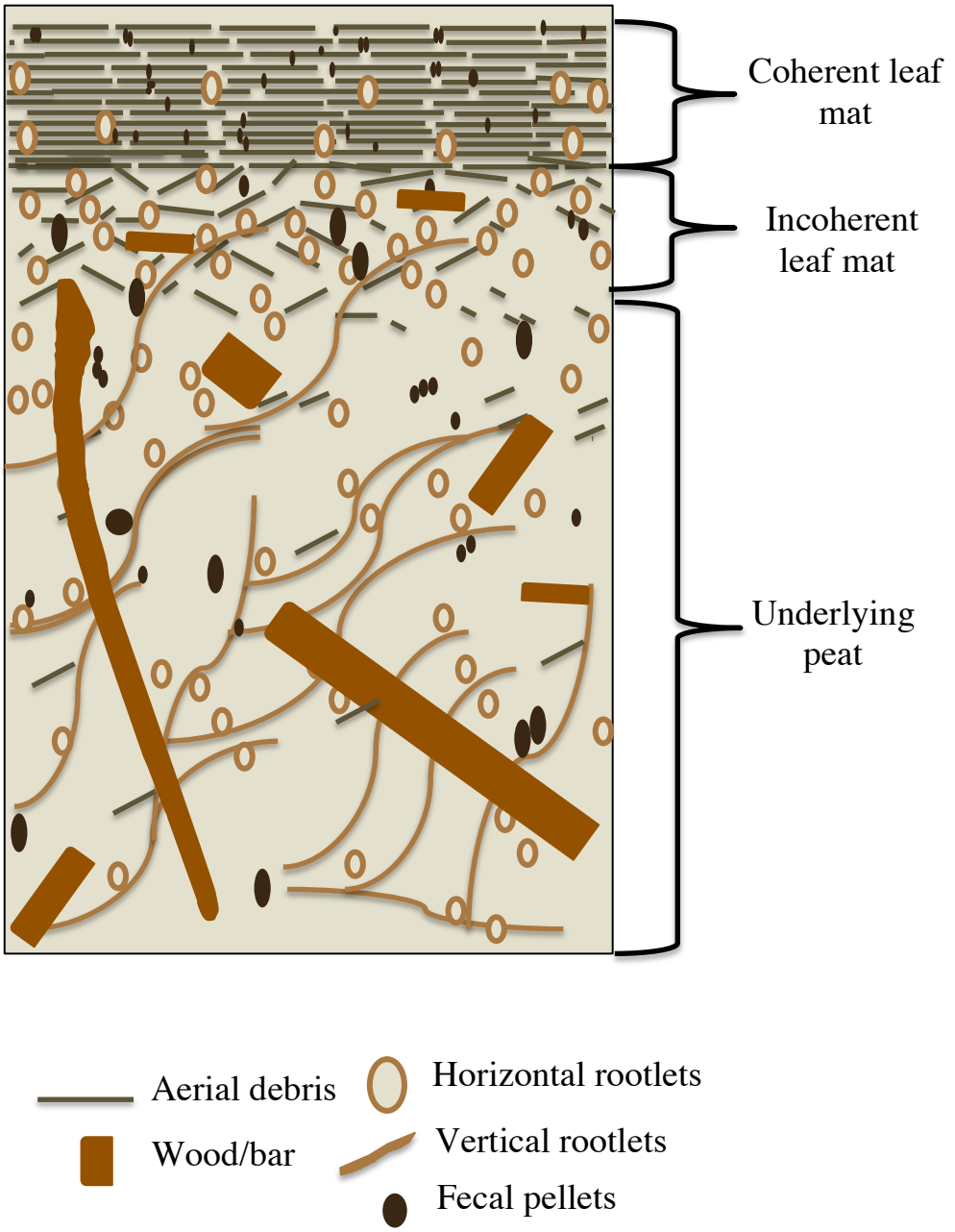


Figure 1: Taphonomically Active Zone (TAZ) of Barnes Sound Peat.
The TAZ consists of the coherent, incoherent, and underlying peat. Each increment's composition is schematic shown.

spectacular examples of ephemeral plant organs and tissues preserved such as aerenchyma, leaf mesophyll, pollen with pollen tubes, and seeds with embryos.

2.2 Peat Taphonomy

Cohen and Spackman (1977) were among the first American coal petrologists to reinvestigate the link between peat and coal since European coal petrologists in the 1930s, and were also among the first to consider the link between plant organs and tissue with coal petrology. In their investigation of modern subtropical peat, specifically from the Okefenokee Swamp and the Florida Everglades, they defined peat composition into matrix and framework. They divided framework components into two categories, distinguishing between root (non-sedimentary) and shoot (sedimentary) components. Peat matrix as particles with all dimensions less than 100μ and peat framework as particles with one dimension greater than 100μ (Cohen and Spackman, 1977). In modern peat, the framework to matrix and shoot-to-root ratios distinguish mangrove from freshwater peat: mangrove peat has a high framework- to-matrix ratio and a low shoot-to-root ratio, while a freshwater peat has a low framework-to-matrix ratio and a high shoot-to-root ratio (Cohen and Spackman, 1977).

Raymond (1987) used Cohen and Spackman's peat composition ratios (framework-to-matrix and shoot-to-root) to evaluate surficial mangrove peat from the Ten Thousand Islands section of Everglades National Park. Using modern peat composition ratios can thus predict taxonomic composition. Raymond (1987) used this conclusion to apply to Pennsylvanian permineralized peats. In agreement with Cohen and Spackman (1977), Raymond (1987) found low percentages of aerial debris in

mangrove peat, but noted that Cohen and collaborators may have underestimated the amount of framework in peat because their sampling method limited them to peat components approximately one centimeter or less in diameter (Cohen and Spackman 1976; Cohen and Spackman, 1977). Raymond and co-workers observed that freshwater peat had significantly higher shoot-to-root ratios than mangrove peat and used these ratios to place most Pennsylvanian coal-ball peat in freshwater depositional settings (Raymond, 1987, 1988; Raymond et al. 2010). Results of this and other studies suggest that with fewer detritivorous crabs thick leaf mats can accumulate in marine mires, the taphonomic criteria used to identify fossil mires as freshwater or marine require reevaluation.

Shearer et al. (1995) discussed the relationship between the evolution of mire forest ecosystems and changes of coal bed thickness and composition. Compared to older coal deposits from the Paleozoic and Mesozoic, Cenozoic coal beds are much thicker, and do not contain vitrain bands (derived from large pieces of wood or *Lycopsid* periderm). Shearer et al. (1995) attributed these differences to increases in productivity of forest ecosystems over time, coupled with changes in the composition of wood (angiosperm wood has less lignin than conifer wood), and increased nutrient cycling. The observation of Shearer et al. (1995) indicates the importance of decomposition pathways in peat accumulation and its effect on coal deposition and composition.

2.3 Leaf Mats

Leaf mats at the mire surface rarely occur in the fossil record. Leaves decay quickly; for example, Raulerson (2004) reported leaf turnover values of 10 weeks to 6

months in the surface litter of Florida mangrove mires. Since mangrove peat accumulates at the rate 8 to 12 cm per 100 years (Ellison and Stoddart, 1991), few leaves persist long enough to be buried by the process of peat accumulation. Leaf mats might be covered and preserved in catastrophic sedimentation events; however, because they form at the surface and consist of particles (leaves, twigs, and flowers, cones, seeds and pollen) with relatively low density, a small flooding event can remove the leaf mat. Leaf mats preserved in Late Paleozoic coal balls are a notable exception to this rule. The thickest recorded cordaitean leaf mat is 10 cm thick; medullosan and tree fern leaf mats are both rare compared to cordaitean leaf mats; lycopsid leaf mat thickness has not been investigated (Raymond et al., 2001). The preservation of thick leaf mats in Late Paleozoic coal balls relates in part to the permineralization process, which enabled preservation of leaf mats via *in situ* cementation. Coal balls are laggerstatten, which provide us with a snapshot of Late Paleozoic leaf mats. Further, because leaf structure has not changed significantly since the Late Paleozoic (veins, spongy and palisade mesophyll, epidermis, cuticle: Raymond et al., 2001), It is possible to track changes in peat taphonomy over time by comparing Late Paleozoic to modern leaf mats. The goal of this contribution is to provide a better understanding of the distribution of leaves, woody roots, rootlets, fecal pellets and matrix in modern peat to enable comparisons between ancient and modern leaf mats, and help identify better depositional analogues for Pennsylvanian permineralized peat.

Based on their observation of modern mires in the Rajang River delta (Sarawak, East Malaysia), Gastaldo and Staub (1999) proposed ancient leaf mats most likely

accumulated and were preserved in small 'lenticular pools' formed from surrounding tree fall depressions. Likewise, Cohen and Spackman (1977) attributed high percentages of aerial debris in freshwater *Myrica-Persia-Salix* peat to standing water. Raymond et al. (2001) noted the presence of roots and rootlets in nearly all permineralized leaf mats from the Pennsylvanian. Because plants do not send roots into anoxic, waterlogged substrates (Smirnoff, and Crawford, 1983), Raymond and collaborators suggested that these permineralized leaf mats formed in peat above the vadose zone, putting the taphonomic active zone above the vadose zone. Due to the high porosity associated with the preservation of pristine leaf mats in Pennsylvanian coal balls, coal balls most likely formed near the surface of the mire, i.e. in the TAZ of mire environments (Raymond et al., 2012).

2.4 Mangrove Productivity Studies

In modern mangroves, a variety of terrestrial micro-invertebrates (beetles, flies, modern roaches, termites) and macro-invertebrates (decapods, amphipods, neogastropods) contribute to the decomposition of organic debris (Dey, 2010; Middleton and McKee, 2001; Nagelkerken et. al, 1989).

Terrestrial arthropods (mites, millipedes, insects) radiated in the Devonian and contributed to decomposition in Paleozoic mires; however the terrestrial arthropod community has changed radically since that time (Scott and Taylor, 1983; Raymond et al. 2001; Grimaldi and Engle, 2005). Swift et al. (1979) emphasized that micro-detritivores are an important factor in altering modern peats, but relatively few studies focus on the micro-invertebrate communities of tropical and subtropical wetlands.

Scott and Taylor (1983) investigated the potential micro-arthropod community of a Carboniferous mire from Lewis Creek, Kentucky by using the analysis of coprolites and evidence from preserved aerial debris. Their findings indicate that edge feeding (a type of herbivory) has been around since the Paleozoic. The micro-arthropod community was made up of primitive mites and collembolans that exhibited the most common plant-animal interactions preserved in the permineralized peat followed by millipedes, cockroaches, grasshoppers, and crickets.

Dey (2010) investigated micro-arthropod diversity and community structure over a 30-month period in West Bengal. Dey (2010) discovered that the community consisted of 27.3% *Collembola,* 10% *Coleoptera,* 5.7% *Diptera*, 5.1% *Isopoda*, 5% *Hymenoptera*, and 10.6% other arthropods (spiders, centipedes, millipedes). The highest diversity and abundance of micro-arthopods coincided with the time at which decomposing litter had the most nutrients, which was approximately six months after litter fall. Diversity and abundance also fluctuated with the rainy season, having the highest values right after the monsoon season.

Frouz et al. (2004) investigated the diversity and abundance of terrestrial arthropods on a moisture gradient from the center of a local lake in central Florida to an upland hummock. They found that the amount of organic matter, the ability of the soil to keep moisture, and the amount of flooding were the major factors controlling the diversity and abundance of the soil arthropod communities. Arthropods need moisture to survive, therefore with the ability of soil to maintain moisture being the most important factor. The highest abundance of soil arthropods occurred at the center of the gradient;

however, there seemed to be no correlation between specific species and moisture along the gradient. All soil arthropods concentrated near the surface of the soil and only were found deeper when moisture was readily available. Compared to Dey (2010), *Isopoda* and *Diptera* were the most abundant arthropod orders. Dey 2010) and Frouz et al. (2004) suggest that soil arthropods play an important role in the taphonomic active zone of these disparate terrestrial environments. Both agreed that moisture availability contributes to micro-arthropod abundance and diversity. An extensive study of arthropod communities in mangrove environments and how salt fluctuations affect their diversity and abundance has yet to be performed.

Macro-detritivores are also an important part of decomposition pathways in mangrove systems. Cohen and Spackman (1977) and Esterle (1990) noted that crabs consumed leaves in brackish mires, but did not consider their role in altering peat composition. Another macro-detritivore that is overlooked in peat taphonomy is amphipods (Middleton and McKee, 2001).

However, research over the past 30 years on mangrove productivity and nutrient cycles reveals the important role of crabs in consuming aerial debris in brackish and fully marine mires (Lee, 1989; Robertson and Daniel, 1989; Robertson et al., 1992; Smith et al., 1991; Alongi, 2009). Ocypodid crabs consume mangrove litter in South American and Caribbean mangrove forests; and terrestrial herbivorous and detritus-eating snails (such as *Melampus coffeus* and *Nassarius vibex*) play a significant role in litter recycling as well (Nagelkerken et al., 1989; Middleton and McKee, 2001; Proffitt and Devlin, 2005; Nordhaus et al., 2006). An et al., 2014 documented in a southern

China mangrove ecosystem that terrestrial gastropods are a major contribution to the consumption of degraded mangrove aerial debris. However, while the crabs ate mostly leaves, the gastropods mostly ate the crab fecal material for food instead of actual aerial debris.

In Australia, mangrove forests dominated by *Ceriops tagal* and *Brugueira exaristata, detritivorous* sesarmid crabs (specifically *Sesarma fourmonoiri, S. messa,* and *S. smithi)* consume over 71% of the litter fall, while tides exported approximately 25% (Robertson and Daniel, 1989). Significantly more litter accumulated in mangrove forests where sesarmid crabs were rare to absent (Robertson and Daniel, 1989). In another Australian *Avicennia germinans* mangrove forest, ocypodid crabs consumed 32% of the litter fall and the tide exported another 21% (Robertson and Daniel, 1989).

In the Western Hemisphere, specifically the Florida Gulf Coast, the Caribbean, and the eastern coasts of Central and South America, detritivore sesarmid crabs are rare. The most abundant sesaramids, (*Aratus pisonni*) can be herbivorous, preferring live mangrove leaves in the canopy (Erickson et al, 2003). When *A. pisonni* consumes leaves in the canopy, it will eat approximately only 30% of the leaf and leave the rest (Erickson et al, 2003).

The ocypodid crab *Ucides cordatus* and the grapsid crab *Goniopsis cruentata* are the most important mega-detritivores in New World mangrove communities (Middleton and McKee, 2001; Nordhaus and Wolf, 2007). In mangrove mires with few detritivore grapsid and ocypodid crabs, it may be possible for mangrove leaf mats to accumulate (S. Davis, 2014, pers. comm., 19 December).

2.5 The Role of Grapsid and Ocypodid Crabs in Modern Mires

The radiation of grapsid and ocypodid crabs could have had a significant effect on the taphonomy of mangrove leaves. Nutrient recycling in mangrove ecosystems is promoted by their feeding styles. They burrow and move through the sediment, chemically and physically changing it (Kristensen et al., 2008, Nagelkerken et al., 1989). Ocypodids are not as reliant on mangrove carbon as sesaramids are, mostly eating microphytobentos for nutrients (France, 1998, Meziane et al., 2002).

Mangrove crabs today live in intertidal locations, and have a poor fossil record (Feldmann and Schweitzer, 2006). However, the earliest undisputed crabs appeared in the early to mid-Jurassic (Schweitzer and Feldmann, 2010). The earliest ocypodid and grapsid crabs, which include the sesarmids, date to the late Eocene-Oligocene (ocypodids, Barnes, 1968; grapsids, Glaessner, 1969). The precise geographic distribution of ocypodid and grapsid crabs in mangrove systems is still far from being completely understood. However mangrove crabs together with neogastropods are the most common terrestrial macro-organisms in intertidal mangrove communities (Nagelkerken et al., 1989). Sesarmids are most common in Southeast Asia, and not nearly as common in North and Central America; currently only 5 species of grapsids have been identified in the New World (Abele, 1992 and Erickson et al., 2008).

Sesarmidae, family of crabs a part of the superfamily *Grapsoidea,* are among the most reliant on mangrove carbon (Nagelkerken et al. 1989). Along with deposit feeding and detritivory sesarmids and ocypodids can be herbivores. While *Ocypodidae* are generally detritivorous, grapsid crabs such as those from the family *Sesarmidae*

scavenge animal matter or are sometimes predators (Beever et al, 1979; Erickson et al, 2003; Erickson et. al, 2008). *Aratus pissoni* are generally herbivorous crabs (Erickson et al., 2003). Crabs such as *Ucides cordatus* and *A. pissoni* from Brazil almost eat entirely aerial plant (Erickson et al., 2003 and Nordhaus, 2004). They are found dwelling in the canopy usually on top or hanging from mangrove leaves. *A. pissoni* eats red mangrove leaves off the canopy by scraping away the leaf's surface, but prefers other means of nutrients. These New World crabs are commonly found on the Gulf Coast of Florida, including the field site at Barnes Sound.

3. FIELD SITES AND METHODS

3.1 Field Site Description and History

Surficial mangrove peat from Barnes Sound on Key Largo in the Upper Florida Keys was sampled (Fig. 2). Barnes Sound has a subtropical climate and experiences microtidal flushing with a tidal range of approximately 8 cm. The Key Largo climate conditions were extrapolated from NOAA and National Weather Service climate data from Tavernier, FL less than 30 miles from the field location (Florida Keys: National Weather Service Forest Office, 2000).

Figure 2: Field Location: Barnes Sound, Key Largo, Florida.

Ishman et al. (1998) traced the ecological history of the Barnes Sound area based on modern faunal and floral distributions from a sediment core (MB1) from the center of the sound. Barnes Sound, before 1850, was most likely a freshwater environment, becoming brackish to marine in the early 1900's. Based on MB1, Ishman et al. (1998) stated that Barnes Sound has an average sedimentation rate of 0.80 cm per year. The modern salinity varies from 14-45 ppt (brackish to hypersaline). The C111 canal built northwest of Barnes Sound in 1968, which deflects freshwater from entering the sound, may contribute to the wide range in salinity. Changes in faunal and floral communities in MB1 reflect a general rise in sea level, as well as an increase in salinity in this area for the last 150 years (Ishman et al., 1998). Although increased urbanization has impacted much of southern Florida, Barnes Sound remains relatively undeveloped compared to other parts of the Florida coast due to its isolated location. Since the 1980's, hypersaline conditions have decreased. This is most likely due to changes in the configuration of the C-111 canal allowing natural freshwater flooding to occur (Ishman et al., 1998).

The basin mangrove mire has two mangrove species: *Rhizophora mangle* (red mangrove) and *Avicennia germinans* (black mangrove) ranging from less than one meter to 4 meters tall. Most of the trees in the vicinity of the sampling site were *R. mangle*; however pneumatophores of *A. germinans* occurred near all coring sites. Peat cores from Barnes Sound have red tannin-rich coloring of *R. mangle* peat, consistent with the dominance of *R. mangle* at the collecting site.

A thick leaf mat has accumulated on the surface of the mangrove mires at Barnes Sound around the aerial roots of *Rhizophora mangle* and the pneumatophores of

Avicennia germinans. Horizontal rootlets appeared at the surface of the peat growing across leaves.

Presence of crab activity was not observed while visiting the field site: no crabs in trees or burrows on the forest floor. According to Beever et al. (1979), finding and capturing actual crabs is very challenging since they are hard to find and are very fast. The best way to decide what types of crabs, if any at all, are present is by direct observation of aerial debris.

3.2 Field Methods

Modern leaf mats and the underlying surficial peat were collected using short cores (15 cm diameter, 13.5 cm long). The edge of the coring device cut through leaves, small twigs and roots. A trowel and small hand saw were used to cut through woody debris and large roots that extended beyond the edges of the core. During core extraction, a hand was placed underneath the core to prevent peat loss. After removal from the ground, a mesh bag made of fiberglass screen wire covered each core to prevent loss of debris. The mesh bags allowed cores from submerged locations to drain, but kept the peat moist. After collection, each core was placed in a large plastic bag. There were stored in a dark, air-conditioned room, cores stored in this manner retained their moisture for more than a year.

Five cores (E3ES1-E3ES5) were collected at Barnes Sound: three on hummocks (E3ES1, E3ES2, E3ES5), and two in swales (E3ES3, E3ES4), approximately 540 m southeast from the Barnes Sound shore. Water level was no more than 30 cm deep, for

swales, and hummocks had exposed surfaces. Mangrove mires accumulate at sea level and have almost no topography.

4. LABORATORY METHODS

4.1 Analysis of Cored Peat

In the lab, each core was extruded into a mesh bag made of screen wire in the shape of the core, discarding leaves and leaf fragments stuck to the inside of the core. These were leaves from the surface intruded into the peat by the action of coring. The screen wire bags kept the cores intact but did not prevent the loss of fine particles from the edge of the core.

Each core was described from top to bottom in three increments due to change in peat composition with depth, loosely based on similar coring methods from Chambers et al (2014). Each core increment was examined using a stereographic microscope, noting the presence of visible fecal pellets and aerial debris damage. A subsample from core E3ES5 was taken from the 2.5-5cm increment. The subsample was sieved using 2mm, 1 mm, 500 μm, 250 μm and 106 μm mesh sieves. Each sieved subsample was oven dried for 2 days at 60°C for preparation for SEM analysis. The sieved subsample was used to retrieve representative fecal pellet size distribution. Sample was coated in gold for best resolution for imaging using the TESCAN VEGA SEM with guidance from Dr. Michael Pendleton.

Each core was analyzed by the depth of the coherent leaf mat, i.e. the depth at which entire leaves or large fragments greater than 1 cm^2; the thickness of the incoherent leaf mat, i.e. the depth at which recognizable leaf fragments disappear; the number of vertically stacked leaves in the coherent leaf mat; the presence of horizontal roots and

rootlets; the presence of vertical roots and rootlets, including *Avicennia germinans* pneumatophores.

4.2 Leaf Taphonomy

Although mangrove mires rarely accumulate and preserve aerial debris, at Barnes Sound, the leaf mat is unusually thick. From the five cores, the taphonomic condition of one hundred leaves and leaf fragments were analyzed assigning each leaf to a taphonomic grade ranging from 0-4 (using descriptions listed in Table 1). Photo-documentation on each leaf was performed as well as distinguished, if possible, between micro- and macro-herbivory and micro- and macro-detritivore damage (see Table 2).

Both post-depositional processes (physical degradation, detritivory and microbial attack) and herbivory may contribute to the taphonomic grade of mangrove leaves. Distinguishing between herbivory and detritivory damage types is important in understanding the decomposition pathways that occur at Barnes Sound. Leaves displayed a wide range of damage: skeletonization (all of leaf is destroyed leaving only the veins behind), puckering and wrinkling of the cuticle and epidermis due to lose of mesophyll, destruction of the mesophyll from leaf mining, and destruction of vascular tissue resulting in cuticular bags (all of leaf is destroyed except the cuticle remaining), bleaching, oxidation rinds, scraping, penetration by rootlets and fungal hyphae, and various types of edge feeding. When possible, *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* assembled by Labandeira et al. (2007) to identify herbivory and insect/plant interactions recorded by mangrove leaves. Crab herbivory and detritivory was identified using Erickson et al. (2003) and Middleton and McKee (2001).

5. RESULTS

5.1 Leaf-mat Characterization and Thickness

In all five cores the leaf mat consisted of *Rhizophera mangle* and *Avicenna germinans* leaves, non-woody rootlets, parts of *R. mangle* propagules that showed signs of degradation from possible canopy dwellers, mangrove trunk and branch wood and bark. Well-preserved micro-arthropod fecal pellet accumulations occurred between leaves. Other important animal remains consisted of *Melampus coffeus* and *Nassarius vibex* shells as well as unidentifiable insect parts.

The coherent leaf mat at Barnes Sound is approximately 2.5 cm thick and consisted of 19 to 37 stacked leaves (Table 3). The cored leave mat with the fewest leaves (19) had a large piece of wood below the coherent leaf mat most likely limiting the accommodation space. Leaf-mat thickness from the two shallow swales did not differ significantly from leaf mat thickness on the hummocks. The thickness of the leaf mats on hummocks and in swales did not vary (unpaired t-test with p value of 0.5591).

5.2 Peat Below the Leaf Mat

Below the leaf mat, the peat consists of fragments of leaves and other aerial debris intruded by roots and rootlets, called the incoherent leaf mat. Our description of the incoherent leaf mat reflects the description of degraded leaf mats found in Pennsylvanian permineralized peat described in Raymond et al. (2012). With depth, the rootlets become larger and more numerous, and the coherent leaf mat gives way to root peat. Rootlets started forming approximately halfway down the coherent leaf mat of each

Table 1: Leaf Taphonomic Grade Description

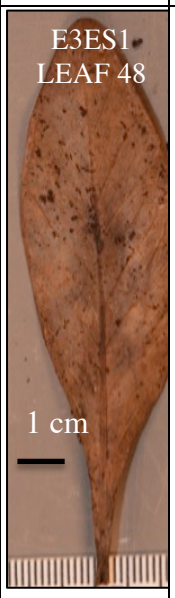
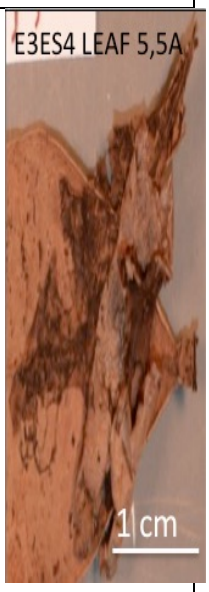
Taphonomic Grade	0	1	2	3	4
Characteristics	Nearly pristine; margin complete; pin holes may be present; little to no fungal attack; leaves may be bleached	Wrinkled cuticle or other signs of attack, or missing epidermis, skeletonization, or holes less that 10% of one side	Curled edges due to missing mesophyll, or missing epidermis or skeletonization, holes, craters, and plates are less than 25% of one side of leaf	Skeletonization, holes, craters & plates cover 50-100% of one side of leaf; skeletonization involves total loss of mesophyll with only the bottom epidermis and major veins remaining	Complete skeletonization or a cuticular bag
Example					

Table 2: Barnes Sound Leaf Damage Types

Taphonomy Observation	Type of Destruction
Scalloped margin (edge feeding)	Micro-herbivory or Micro-detritivory
Scraped cuticle and epidermis from one side of leaf	Herbivory
Hole feeding with oxidation rinds	Herbivory
Epidermis removal	Herbivory
Raised cuticle over midrib	Herbivory (leaf mining)
Patches of Skeletonization	Herbivory (specifically *Aratus pissoni*)
Missing Mesophyll	Insect Herbivory (life mining) or microbial decomposition
Complete skeletonization	Micro-detritivory and Macro-detritivory (specifically *Melampus coffeus*)
Edge feeding leaving petioles and the main rib of the leaf behind	Macro-detritivory (potentially detritivore crabs)
Cuticular Bag	Microbial decomposition
Bleaching	Microbial decomposition
Wrinkled Cuticle	Microbial decomposition
Leaf craters (galling)	Canopy parasite; either an insect, fungi, bacteria
Leaf plates	Canopy parasite; either an insect, fungi, bacteria

Table 3: Barnes Sound Coherent Leaf Mat Description

Barnes Sound Core	Relative Elevation	Stacked leaves in Coherent leaf mat	Number of Stacked leaves above first living rootlet
E3ES1	Hummock	20	8
E3ES2	Hummock	37	16
E3ES3	Swale	25	13
E3ES4	Swale	19	10
E3ES5	Hummock	23	13

core stated in Table 3. In all the cores, the incoherent leaf mat did not extend past 5 cm (thickness was approximately 2.5 cm). Most of the peat matrix as defined by Cohen and Spackman (1977) (i.e. particles with one dimension ≤100 μ) in Barnes Sound cores was aggregated in fecal pellets.

5.3 Fecal Pellets Size Distribution

Fecal pellets were abundant at all depths in the cores. Fecal pellets were best preserved between stacked leaves within the coherent leaf mat where they often occur in aggregates. SEM images were taken of the sieved subsample from the 2.5-5cm increment from E3ES5 (Fig. 3). Fecal pellets that were larger (1mm and 2mm) look like they were aggregates of other smaller fecal pellets bound together by fungal hyphae and biofilm.

5.4 Leaf Taphonomy

One hundred leaves from the top to the bottom of the coherent leaf mat from E3ES4 (low elevation) and E3ES1(high elevation) were selected for taphonomic grade evaluation using Table 1 and Table 2 for description. The average taphonomic grade for the entire sample was 2.12 and the most frequent taphonomic grade assigned was taphonomic grade 2. Leaves from both cores had a similar taphonomic grade (1.966 with a mode of 1 for the low area; 2.183 with a mode of 2 for the high area) is not statistically significant (unpaired t-test, p value=0.4067).

Labandeira et al, (2007) was used to identify damage types that are common to mangrove and freshwater habitats. Three damage types not listed by Labandeira et al.

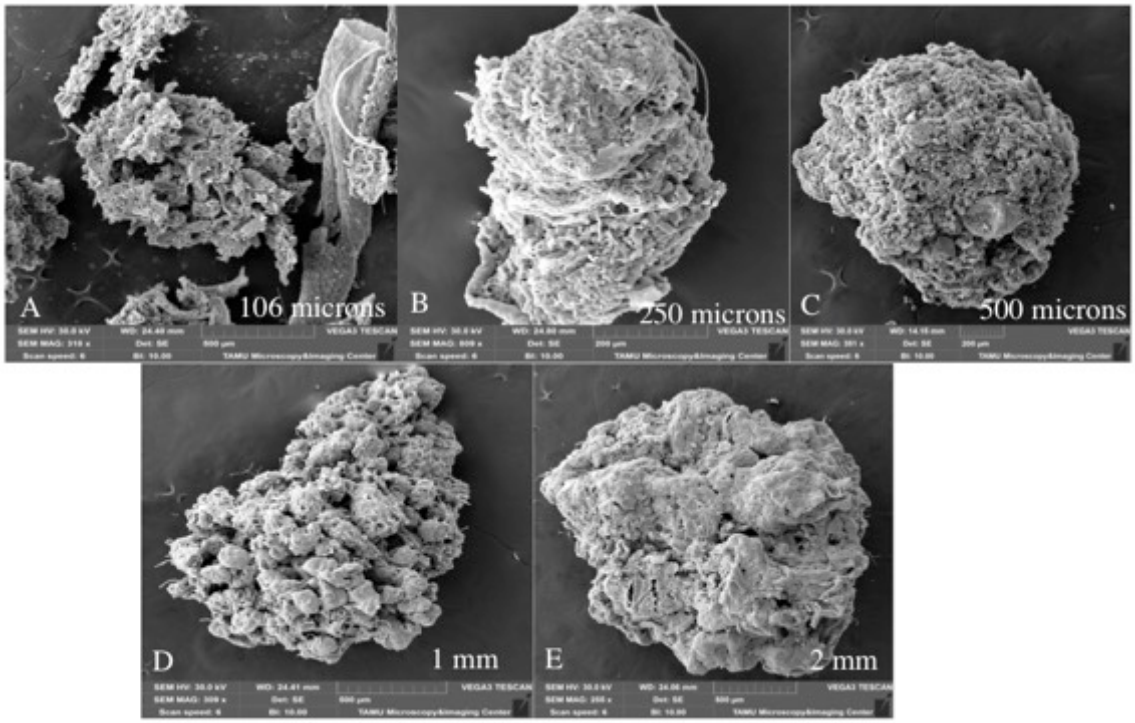


Figure 3: SEM Images from E3ES5 (2.5-5 cm increment). A) Fecal pellet with fungal hyphae with rootlet at 106µ, B) Fecal pellet with fungal hyphae and biofilm at 250µ, C) Fecal pellet with fungal hyphae at 500µ, D) Fecal pellets aggregated together by fungal hyphae and biofilm at 1mm, E) Fecal pellet covered in biofilm and fungal hyphae at 2mm

(2007) occurred commonly at Barnes Sound: 1, as described by Cohen and Spackman (1977) and Gastaldo and Staub (1999) leaves reduced to cuticular bags; 2, scraped and eaten the cuticle and epidermis from one surface of leaves by *Aratus pissoni* while still attached to the tree, occasionally creating a hole (Erickson, 2003); 3, Edge feeding by possible detritivore crabs or neogastropods (Middleton and McKee, 2001). Table 2 lists the damage types encountered and the probable causes of each type: micro- and macro-herbivory, parasitism, macro-detritivory, micro-detritivory, and microbial attack.

After examining the 100 leaves, fifteen leaves with one sided scraping reflected *A. pissoni's* damage to the leaves in the canopy while only eight leaves had possible signs of macro-detritivory similar to the detritivore crabs in Belize described by Middleton and McKee (2001). Examples of potential crab damage (both detritivory and herbivory) are shown in Figure 4. Complete skeletonization can occur from insects as well as *Melampus coffeus* (Proffitt and Devlin, 2005); therefore, figuring out which skeletonized each leaf is nearly impossible. Most leaves reflected a combination of herbivory, parasitism, micro-detritivory and microbial attack. Macro-detritivory was rare, but was seen. Leaves with a high taphonomic score (3 and 4) typically experienced more than one type of destruction.

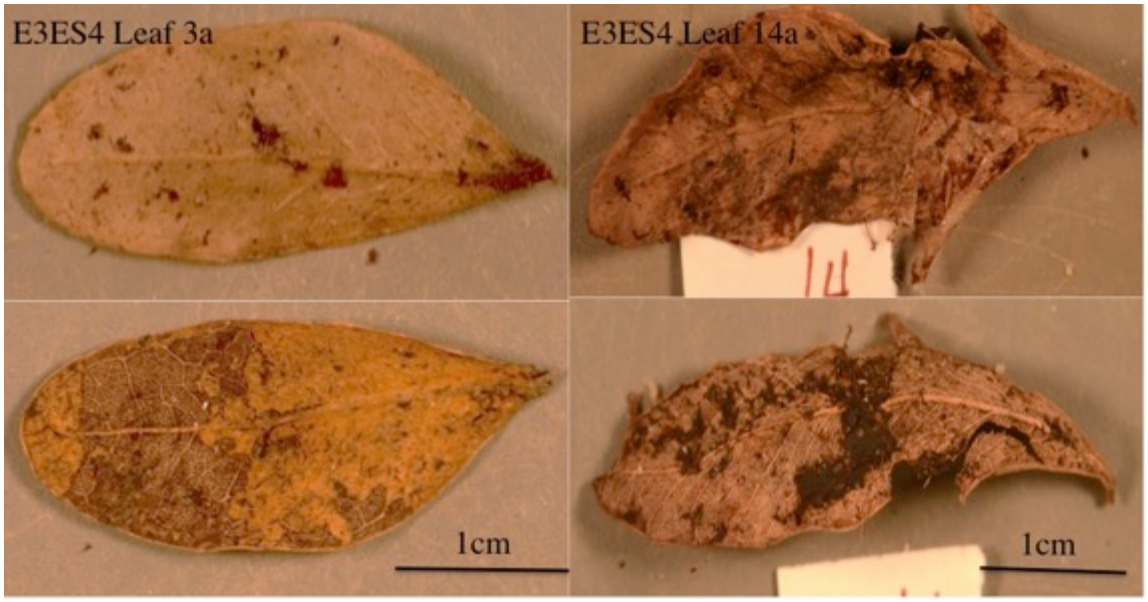


Figure 4: Macro-Herbivory and Detritivory Damage. Left, one sided scraping of leaf similar to *Aratus pissoni*; Right, Edge feeding similar to *Ucides cordatus* and *Goniopsis cruentatis.*

6. DISCUSSION

6.1 Barnes Sound Leaf Mats Record Herbivory in the Canopy

Study of the taphonomically active zone leads to new understanding of decomposition pathways in mangrove systems. Barnes Sound is a rare mangrove mire where thick leaf mats (19 – 37 leaves thick) have accumulated on the peat surface, allowing characterization of taphonomic processes at the peat surface. Previously studied mangrove peat had very little aerial debris accumulation and few leaves, making it difficult to trace taphonomic processes using leaf damage.

Most leaves in the Barnes Sound leaf mat showed multiple types of damage. Much of the damage records canopy processes, i.e. micro- and macro-herbivory, and insect and fungal parasites forming leaf galls, expressed as craters and plates on the surface of leaves in the leaf mat (Table 2). Removal of the cuticle and epidermis on one side of the leaf by the herbivorous mangrove tree crab, *Aratus pisonii*, seen in 15 of 100 leaves, appears to be a leaf damage type unique to mangrove mires, which may be traceable in the fossil record. Beever et al. (1979) also used characteristic damage patterns to establish the presence of *A. pisonii* in the canopy since trapping them was rather difficult. Leaves that experienced only herbivory and parasitism in the canopy, relatively untouched by detritivory or microbial decomposition on the forest floor, rarely exceed taphonomic grade 2. Johnstone (1981) surveyed leaf damage due to herbivores in a mangrove forest in Papua New Guinea and reported leaf area losses ranging from 0.24 to 14.2% (mean 6.8%). He reported edge feeding, large and small internal holes,

and skeletonization, but did not identify causal organisms. Robertson and Duke (1987) studied insect herbivory in an Australian mangrove forest and found leaf area losses ranging from 0.03 to 35%. Like fossil leaves from terra firma and freshwater mires, leaf fossils from mangrove mires have the potential to preserve ancient plant – insect interactions (Scott and Taylor, 1983; Raymond et al., 2001; Labandeira et al., 2013).

Mangrove peat accumulates in the intertidal zone (Woodroffe, 1993). In Florida, rainfall seasonality probably prevents mangrove peat from accumulating above the intertidal zone mostly likely causing the peat to dry out. Although the shallow swales in the mire surface experience more inundation than the slight hummocks, the entire surface of the mire is inundated in high tides. Microbial decomposition results in the formation of 'cuticular bags' and bleaching of the leaves, in which the mesophyll and veins of the leaf decompose, leaving the decay resistant cuticle behind. In other mire habitats, cuticular bags commonly occur in submerged sites (Gastaldo and Staub, 1999; personal observation of Corkscrew Swamp Sanctuary). Therefore, bleaching and the formation of cuticular bags most likely occurred while the leaf was very wet or submerged. DiMichele et al. (1984) described 'paper coal' from the Pennsylvanian of Indiana composed primarily of *Karinopteris* (seed fern) leaf cuticle. This deposit and other paper coals may result from microbial decomposition of leaves in standing water.

Leaf mats and the underlying peat showed signs of micro- and macro-detritivores in the form of *Melampus coffeus* shells (coffee bean snail), fecal pellets, ranging from 106 μm to 2 mm in diameter, and damaged leaves. The most important detritivores in Caribbean and Central American mangrove mires are the detritivorous mangrove crabs

(*Goniopsis cruentata* and *Ucides cordatus),* a neogastropod (*M. coffeus),* and an amphipod (*Gammaridea*; Middleton and McKee, 2001; Raulerson, 2004).

Detritivorous mangrove crabs attack the leaf lamina, leaving the petiole and lower parts of the midrib intact (Middleton and McKee, 2001; Raulerson, 2004). These crabs accounted for most leaf decomposition in three Florida mangrove mires (Raulerson, 2004). Most studies of mangrove leaf detritivory by crabs, including Raulerson (2004), used the density of crab burrows to indicate the importance of crabs in macro-detritivore community. No crab burrows were observed at Barnes Sound. However, 8 of 100 mangrove leaves showed signs of crab detritivory (Fig. 4), suggesting that these crabs are present, albeit rare, at the study site.

Melampus coffeus is present based on how common their shells were in all 5 cores. However, to distinguish what damage types are associated with them is very difficult since they scrape leaves, resulting in complete skeletonization very similar to that of micro-detritivorous insects (Raulerson, 2004). Skeletonization can happen in the canopy due to herbivory as well as on the mire floor, but extremely fragile completely skeletonized leaves may be characteristic of *M. coffeus* detritivory. Proffitt and Devlin (2005) performed a tethered leaf case experiment in Boca Ceiga Bay, Florida, and *M. coffeus* consumed 40.5% of litter fall. However, An et al. (2014) studied detritivorous gastropods in a mangrove in southern China and reported that they preferred to consume crab fecal material for nutrients rather than the aerial debris itself.

Amphipod parts were not observed in the core; insect parts were relatively common. Nonetheless, fecal pellets reflect presence of a wide range of micro-arthropod

detritivores, including marine amphipods, and perhaps oribatid mites and collembolans as well. The terrestrial micro-arthropods of Caribbean mangroves are poorly known. Dey (2010) studied the terrestrial micro-arthropod community of an Indian mangrove mire, and *Collembola* and *Coleoptera* were the most common. Frouz et al. (2004) studied a freshwater location in central Florida and reported that *Isopoda* and *Diptera* were the most common arthropod orders.

Once on the forest floor, leaves attacked in the canopy may be vulnerable to faster decomposition than pristine leaves. For example, *Aratus pissoni* attack removes the cuticle and epidermis leaving the mesophyll vulnerable to microbial decomposition. Leaves missing the epidermis and cuticle on one surface sometimes had exposed veins and little brown shriveled cubes of organic matter in place of the mesophyll.

Generally, leaves decay through microbial decomposition and form leaf cuticular bags in a moist environment. In non-submerged locations, leaves are destroyed by arthropod detritivores (beetles, flies, modern roaches, or termites) causing leaves to become skeletonized or become shredded. Potential examples of crab detritivory were seen on only eight leaves out of the 100 examined. Leaves that did exhibit potential signs of crab detritivory (large pieces missing from edge feeding with the petiole and main rib untouched) are similar to what Middleton and McKee (2001) described.

Agreeing with Labandeira et al. (2007), leaf mats best preserve the animal-plant interactions occurring in the canopy. Evidence of herbivory is not destroyed due to the detritivorous crabs at Barnes Sound that is greatly reduced compared to other previously

studied subtropical and tropical mangrove sites. Therefore, aerial debris can accumulate thick leaf mats with the absence or reduction of macro-detritivores.

6.2 Leaf Mat Results Compared to Previous Research

A mangrove mire on Twin Cays west of Belize, aerial debris degraded three times faster when crabs and amphipods were present. Therefore, peat formation in Twin Cays was mostly made of plant tissue grown below ground (i.e. roots) rather than any aerial debris (Middleton and McKee, 2001). Raymond (1987) and Gastaldo and Staub (1999) have analyzed leaf-mat thickness of modern saltwater environments. Raymond (1987) also analyzed the thickness of cordaitean leaf mats in permineralized peat from the Williamson No. 3 coal balls from the Kalo Formation. Leaf-mat thickness from Barnes Sound, Ten Thousand Islands Section of Everglades National Park and the Kalo Formation (Raymond,1987), and East Malaysia (Gastaldo and Staub,1999) are graphed for comparison (Fig. 5) .

Leaf-mat data from the Ten Thousand Island Section of Everglades National Park ranged from 1-8 stacked leaves (Raymond, 1987). Leaf-mat data from the Rajang River Delta in East Malaysia averaged 3-5 leaves with a maximum thickness of eight stacked leaves (Gastaldo and Staub, 1999). Permineralized leaf-mat data from the Kalo Formation had of 3-78 stacked leaves (Raymond, 1987). Leaf-mat thickness from Barnes Sound compared to modern leaf-mat thicknesses from Raymond (1987) and Gastaldo and Staub (1999) is much thicker and extremely statistically significant (unpaired t-test; Raymond, 1987- $p=0.0001$; Gastaldo and Staub, 1999- $p=0.0001$). Leaf-mat thickness

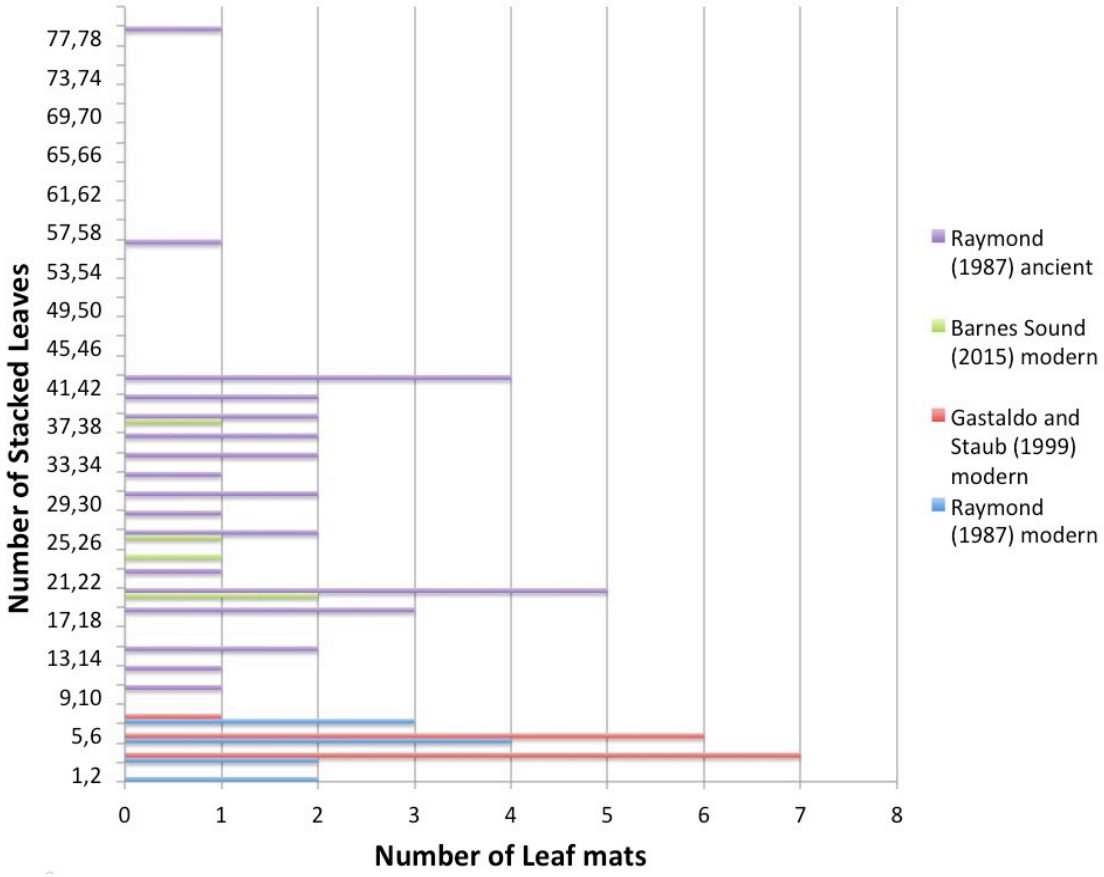


Figure 5: Leaf-mat Thickness Comparison. Number of leaf mats represents each cored leaf mat in study, and the number of stacked leaves represents thickness of cored leaf mat.

in Barnes Sound compared to ancient leaf-mat thickness from Raymond,(1987) are not statistically different (unpaired t-test with p=0.5135).

These results suggest that the modern data collected by Gastaldo and Staub (1999) and Raymond (1987) were taken from field locations with an abundant and diverse detritivorous crab community. Leaf mats that are thin exhibit tidal export and a detritivorous crab community. Barnes Sound's leaf mats are as thick as ancient cordaitean leaf mats in terms of the number of leaves stacked. This indicates that the thickness of leaf mats is not restricted to freshwater accumulation. If Late Carboniferous cordaitean leaf mats accumulated in saltwater, their thickness is consistent with the absence of macro-detritivores in Late Paleozoic mangrove swamps. Thick cordaitean leaf mats support the idea that the evolution of ocypodid and grapsid crabs changed the likelihood of preservation in marine mires.

6.3 Evolution of Modern Crabs: A Change in the Taphonomic Potential

Results of this study suggest that the appearance of ocypodid and grapsid crabs in the Late Eocene – Oligocene constitute a major taphonomic change in marine mires (ocypodids, Barnes, 1968; grapsids, Glaessner, 1969). Prior to the appearance of these organisms, the shoot-to-root ratios and leaf-mat thicknesses of freshwater and mangrove peat may have had been more similar. In the absence of mangrove crabs, early mangrove communities would have exported more leaves to the open ocean or retained more buried leaves in peat and organic-rich muds. In terrestrial ecosystems, including mires, detritivores enhance the rate of nutrient recycling and thus, productivity by

shredding debris that increases the surface area of debris particles relative to volume enhancing rates of microbial decomposition (Swift et al., 1979; Lavelle et al., 1993).

6.4 Implications for Carboniferous and Modern Mire Environments

In their comparison of mangrove and freshwater peat, Cohen and Spackman (1977) reported that mangrove peat consisted primarily of root debris, due to rapid decomposition in mangrove mires and tidal export of aerial debris (see also Raymond, 1987; Covington and Raymond, 1989). Subsequently, the presence of thick leaf mats and abundant aerial debris in many Pennsylvanian permineralized peats has been used as evidence for accumulation in freshwater (Phillips et al., 1985; Raymond, 1988, DiMichele and Phillips, 1994). For example, Raymond et al. (2001) reported a Pennsylvanian leaf mat with 77-stacked leaves. Nonetheless, studies of mangrove productivity over the last 20 years stress the role of macro-detritivores, primarily mangrove crabs but also neogastropods, in consuming leaves (Roberson and Daniel, 1989; Osborne and Smith,1990; Smith et al., 1991; Twilley et al., 1997; Middleton and McKee, 2001; Skov and Hartnoll, 2002; Proffit and Devlin, 2005; Nagelkerken et al., 2007; Nordhaus and Wolff, 2007;Alongi, 2009). Results of this study indicate that thick leaf mats can accumulate in modern mangrove mires with few crabs, suggesting that thick leaf mats could also accumulate in ancient saltwater mires prior to the evolution of decapods and neogastropods. The comparison between Barnes Sound leaf mats with permineralized leaf mats from a Pennsylvanian mire (the Williamson No.3 deposit, Kalo Formation, Iowa) suggests that the two samples cannot be distinguished based on the

number of leaves in the leaf mat. The high percentage of aerial debris in Pennsylvanian permineralized peat is probably not evidence for accumulation in freshwater mires.

Recent studies of the carbonate petrology and geochemistry of Williamson No. 3 coal balls from the Kalo Formation as well as coal balls from Finefrau Nebenbank and Katharina Formation in western Germany both support this conclusion. In the Williamson No. 3 coal balls, high-Mg calcite was the first cement that formed around the preserved plant parts. Modern saltwater calcite precipitates form 11 to 19 percent magnesium carbonate and has high levels of strontium (12200 to 1500 ppm; Raymond et al., 2012; Flugel and Munnecke, 2010; Tucker and Wright, 1990). With the earliest cement being high-Mg calcite, it was potentially a marine water influx that caused coal balls to be formed. However, low-Mg (associated with meteoric diagenesis) is very common in coal balls, causing stable isotope analyses to associate coal balls with freshwater environments (Raymond et al., 2012; Anderson et al., 1981; DeMaris, 2000; Zodrow and Cleal, 1999; Zodrow et al., 1996). However, since coal balls most likely formed near the surface in the taphonomic active zone above the vadose zone, calcite that is most prevalent in coal balls was most likely replaced by low-Mg calcite suggesting meteoric diagenesis, and does not necessarily suggest that the low-Mg is freshwater in origin. Richer et al. (2014) research on coal balls from Finefrau Nebenbank and Katharina Formation are made of fibrous dolomite suggesting that a saltwater source had to be supplied to the formation. Richter et al. (2014) agrees with Raymond e. al. (2012) in that the potentially some coal balls formed in saltwater environments that are

made of fibrous original dolomite agreeing that a saltwater source had to supply the coal balls with high-Mg calcite.

7. CONCLUSIONS

Surficial mangrove peat from Barnes Sound preserves very thick leaf mats (19-37 stacked leaves, 2.5 cm thick) with intruded (live) rootlets approximately 1 cm from the surface. In addition to leaves, the surficial leaf mat also contained fragmented *Rhizophora mangle* propagules, twigs, and bark, fecal pellets, insect parts, and snail shells (*Melampus coffeus* and *Nassarius vibex*). The incoherent leaf mat below the coherent leaf mat extends to a depth of approximately 5 cm, and consists of degraded and fragmented leaves intruded by living horizontal and vertical rootlets, forming a dense network. Short cores (13 cm deep) collected at Barnes Sound indicate that the peat below the coherent and incoherent leaf mat consists primarily of living and dead roots and rootlets, large pieces of wood, and fecal pellets.

Taphonomic analysis of 100 leaves from the coherent leaf mat at Barnes Sound indicates that fallen leaves record canopy herbivory and parasitism, as well as the decomposition pathways occurring on the mire surface: microbial decomposition and detritivory by snails (*Melampus coffeus*) and crabs (presumably, *Ucides cordatus* and *Goniopsis cruentata*). The average taphonomic grade (0-4) is 2.12 with the mode being taphonomic grade 2.

Canopy herbivory and parasitism are most prominent leaf damage types found on leaves. Fifteen leaves showed one-sided scraping attributed to the mangrove tree crab *Aratus pissoni.* Insect parts in the peat probably derive from canopy insects. Microbial attack was evident in loss of leaf tissue (mesophyll and veins) as well as fungal hyphae

interwoven and growing through the coherent and incoherent leaf mat. Abundant fecal pellets, edge feeding, and skeletonization in the coherent and incoherent leaf mat indicate the importance micro-detritivores. Some of these fecal pellets almost certainly derive from amphipods (Middleton and McKee, 2001). Others may derive from groups associated with detritivory in freshwater mires (oribatid mites, collembolans); however, the micro-arthropods of south central United States are poorly known. Shells belonging to the detritivorous neogastropod *Melampus coffeus* occur in the core, but leaf deterioration by these snails is hard to distinguish. Leaves showing attack patterns characteristic of detritivorous mangrove crabs were seen on 8 out of 100 leaves; however, no crab burrows appeared on the mire surface.

Along with a diverse micro-arthropod community, macro-detritivores (specifically crabs) play an important role in the decomposition pathways in modern mangrove mires. Mangrove peat at Barnes Sound preserves an exceptionally thick leaf mat, possibly due to the scarcity of detritivorous mangrove crabs at this locality. In Indo-Pacific, Brazilian, and Belizean mangrove forests, detritivorous mangrove crabs consume a significant percentage of the aerial debris. If crabs are reduced or absent, thick leaf mats can accumulate in saltwater mires (Middleton and McKee, 2001).

The earliest fossils of detritivorous mangrove crabs date to the Late Eocene or Early Oligocene. Our results suggest that in the absence of these and similar macro-detritivores, thick leaf mats could have accumulated in ancient saltwater mires. Therefore, low shoot-to-root ratios and the presence of thick leaf mats cannot be confidently used as taphonomic indicators of freshwater peat. This result supports the

hypothesis of Raymond et al. (2012) and Richter et al. (2014) that the initial carbonate cements in coal balls (Magnesium calcite and dolomite) indicate formation in marine mires.

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